PREDATION ON *KOSMOCERAS* BY SEMIONOTID FISH IN THE MIDDLE JURASSIC LOWER OXFORD CLAY OF ENGLAND

by DAVID M. MARTILL

ABSTRACT. Broken ammonite debris is common in the Lower Oxford Clay and is thought to be attributable in part to the activities of predators. A new specimen of *Kosmoceras* (*Zugokosmoceras*) cf. *obductum* (Buckman) displays a series of bite marks in the region of the peristome suggestive of the dentition of the fishes *Lepidotes*, *Heterostrophus* (Semionotidae) and *Mesturus* (Pycnodontidae).

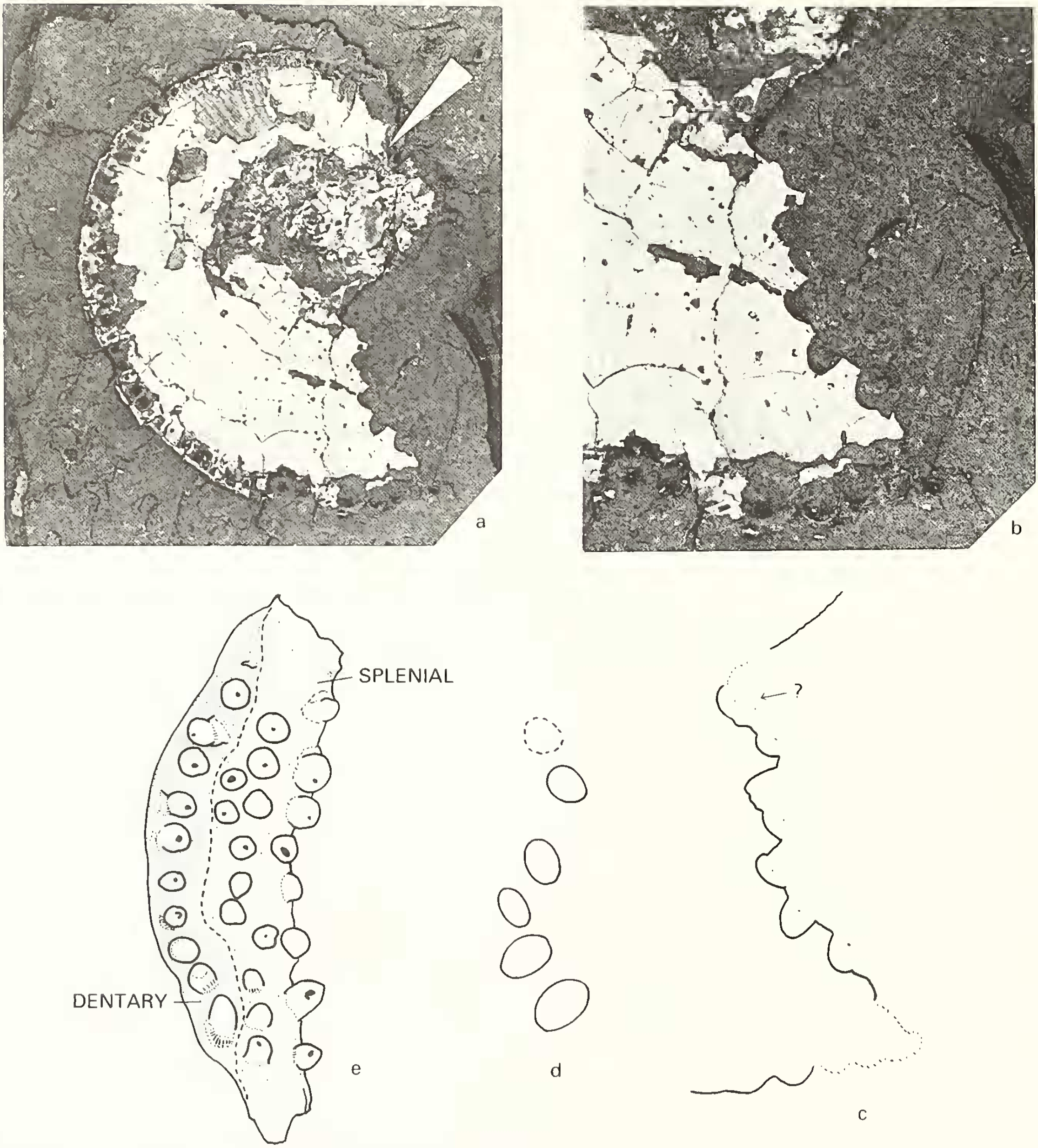
THE ammonite fauna of the Lower Oxford Clay (Middle Callovian, Middle Jurassic) of Peterborough, Cambridgeshire, UK, is remarkable for its exceptional preservation. Although specimens are usually crushed flat, most are preserved in original iridescent white aragonite (Callomon 1968). Species of *Kosmoceras* are most abundant, and include both macroconch and microconch morphs. Many are intact to the peristome, and specimens with extended and complete lappets are numerous. Besides numerous species of *Kosmoceras*, there are also *Erymnoceras* spp., *Binatasphinctes* spp., *Choffatia* sp., *Reineckia* sp., *Hecticoceras* spp. *Sigaloceras* sp. and *Pseudocadoceras* sp. Many of the ammonites are complete, but broken ammonite shell material also occurs in quantity. Shells of the various species of *Kosmoceras* are thin and delicate, and could easily be broken by continued current or storm activity. However, ammonite tests found in storm generated shell beds are often intact and have suffered little from abrasion, suggesting that they are more robust than would at first appear. Much of the broken ammonite debris found must therefore be attributable to the activities of predators rather than to non-biological processes.

DESCRIPTION

The new specimen is a small, laterally compressed phragmacone of *Kosmoceras* cf. *obductum* (Buckman) (text-fig. 1), with the major portion of the body chamber, and a scallop-shaped margin on a slightly damaged peristome. The shell is well preserved, consisting of iridescent white aragonite with a purple sheen. The maximum diameter at the aperture is 50 mm. The specimen was discovered in olive brown bituminous shales at the base of the *K. obductum* Subzone of the *E. coronatum* Zone, at the Dogsthorpe Brick Pit, near Peterborough (Grid reference TF 219019). The specimen has now been protected by a coating of polyvinyl butyral, and is deposited in the collection of the Department of Geology, University of Leicester, accession number LEIUG 99163.

The damaged peristome displays five arcuate incisions, arranged in a semicircle. Each incision is separated by an arc of 3–5 mm from its neighbours. The margin of one incision flaked away after the specimen was collected, reducing the visual impact of the specimen. The incisions have an estimated average diameter of approximately 3 mm, but the shape if complete would have been oval, rather than circular. The arrangement of these incisions is similar to the distribution of teeth (text-fig. 1*e*) on the dentary of the ganoid fishes *Lepidotes* and *Heterostrophus* (Semionotidae) and possibly the maxilla of *Mesturus* (Pycnodontidae).

[Palaeontology, Vol. 33, Part 3, 1990, pp. 739–742.]



TEXT-FIG. 1. *a–d*, *Kosmoceras* cf. *obductum* from the Lower Oxford Clay, Peterborough, with bitten peristome, LEIUG 99163. *a*, phragmacone and body chamber with predator damaged peristome; arrow indicates end of phragmacone, × 1·5. *b*, detail of peristome, approximately × 3·5. *c*, outline of bitten peristome with position of teeth incisions indicated, × 3·5. *d*, position of five teeth which made contact with the ammonite test, × 3·5. *e*, occlusal surface of right lower jaw (here reversed to simulate left jaw) of *Lepidotes macrocheirus*, BM(NH) P6839, Lower Oxford Clay, Peterborough, × 3.

AMMONITE PREDATION

Predation on ammonites has been described by a number of authors (see Lehmann 1976 for a review). Ample evidence that ammonites were victims of predators exists in the form of broken, bitten and damaged tests, but it is often difficult to identify the predators with certainty. Arthropods have been considered to be predators on some Lower Jurassic ammonites, while Kauffman and Kesling (1960) have demonstrated predation by the marine reptile *Mosasaurus*. Small ammonites have been recorded from coprolitic material attributed to plesiosaurs (Wetzel 1960).

Potential predators of ammonites in the Lower Oxford Clay can be found amongst both vertebrates and invertebrates. The large number of belemnites of considerable size (guards up to 30 cm) might be candidates for ammonite predators, as may some of the arthropods. The vertebrate fauna of the Lower Oxford Clay includes a rich diversity of marine reptiles and fishes, but it is only the fishes which have dentitions modified to any degree for coping with hard shell material.

The fish fauna of the Lower Oxford Clay formed the subject of numerous papers by Woodward (1888, 1892*a*, *b*, 1893, 1896, 1928, 1929), but has received little attention since. Fortunately the dentitions of many of the numerous taxa are available for analysis, most housed in the British Museum (Natural History).

Among the fish with durophagous dentitions are the ganoid fishes *Lepidotes* and *Heterostrophus* [= *Dapedium*?] (Semionotidae), *Mesturus leedsi* Woodward (Pycnodontidae), the hybodont shark *Asteracanthus ornatissimus* Agassiz (Hybodontidae), and the chimaeroids *Brachymylus*, *Pachymylus* and *Ischyodus*. The dentition of the chimaeroids is robust, and incorporates large tritoral areas designed to crush shell material. Their sharp mandibular dental plates may have been used to dig for shelled prey. These teeth are unlikely to leave scallop-shaped incisions on any invertebrate test. The dentition of *Asteracanthus* is complex, and comprises a highly heterodont assemblage, although most teeth comprise a broad tritoral area with a well developed central ridge. It is unlikely that *Asteracanthus* would have been capable of producing a crescentic series of incisions. The dentition of the pycnodont *Mesturus* consists of robust, rounded teeth, often with tritoral cusps. Teeth on the splenial and vomer of *Mesturus* are arranged in straight rows (Woodward 1896), and would not produce a crescent-shaped bite. There are four teeth on each premaxilla and dentary of *Mesturus*. They are directed forward and have expanded occlusal surfaces ideal for nibbling small shelly organisms. This dental pattern could produce the pattern of bites seen in the ammonite if all premaxillary teeth from one side, plus one of the premaxillary teeth from the other side of the jaw had made contact with the ammonite test. The dentitions of *Heterostrophus phillipsi* Woodward, 1928, and the three species of Lower Oxford Clay *Lepidotes* (*L. leedsi* Woodward, 1895, *L. macrocheirus* Egerton, 1845 and *L. latifrons* Woodward, 1893) are robust, sometimes peg-like with slightly expanded tips, and well-spaced along the jaw. The dentary is crescentic in occlusal view. Any of these four species could have produced the crescentic bite seen in the ammonite (text-fig. 1*e*).

Alternatives to fish predators are difficult to find preserved as macrofossils in the Lower Oxford Clay. Two arthropods, *Mecochirus* and *Goniochirus*, are common in the same bed from which the ammonite was collected, but both have rather small claws, and those of *Mecochirus* are extremely elongate and delicate, and appear somewhat specialized. Other cephalopods, especially the various naked forms, were possible predators on ammonites, but details of the jaw apparatus in these are poorly known.

DISCUSSION

Lepidotes spp. and *Heterostrophus phillipsi* are the most likely candidates for producing the damaged peristome of the ammonite, but *Mesturus leedsi* cannot be ruled out. *Lepidotes* and *Heterostrophus* are common in the Lower Oxford Clay, but *Mesturus* appears to be rare. Complete specimens are not common, but isolated scales are very abundant. *Lepidotes* is possibly the most abundant large fish in the Lower Oxford Clay, but this is difficult to assess as the robust enamel scales are easy to detect, and have a relatively high preservation potential. No information is available on the level at which *Lepidotes* spp. or *Heterostrophus* lived in the water column, but their general robust fusiform shape, and the massive form of the skull might suggest that they were part of the near benthos biota rather than a part of the surface living community. Perhaps ammonites were also part of the benthic community.

The trophic status of a number of vertebrates from the Lower Oxford Clay has been discussed by Martill (1985, 1987, 1988), but as yet no single account of the interrelationships of the biota is available. This stems mainly from a lack of reliable data. The top of the food chain was dominated by the giant carnivorous reptiles *Liopleurodon* and *Pliosaurus*. There were a number of opportunistic feeders, including the marine crocodilian *Metriorhynchus* which fed on giant fish and hookleted cephalopods (Martill 1987). Many of the vertebrates were highly specialized feeders; the ichthyosaur *Ophthalmosaurus* is thought to have fed exclusively on naked cephalopods, while the marine crocodile *Steneosaurus* and the long necked plesiosaurs were probably mainly fish and naked cephalopod feeders. The fish fauna displays similar trophic niche partitioning. The giant pachycormid *Leedsichthys* was a plankton feeder (Martill 1988), while the other pachycormids *Hypsocormus* and *Asthenocormus* were active predators on smaller fish. Clearly the Lower Oxford Clay food web was highly complex.

Acknowledgments. Thanks go to the London Brick Company for permission to visit the Dogsthorpe Brick Pit, to Alan Dawn for help in excavating the site, and to Colin Patterson (BMNH) for permission to examine material in his care.

REFERENCES

CALLOMON, J. H. 1968. The Kellaways Beds and the Oxford Clay. 264–290. *In* SYLVESTER BRADLEY, P. C. and FORD, T. D. (eds.). *The Geology of the East Midlands*. University of Leicester Press, Leicester, 400 pp.

EGERTON, P. G. 1845. On some new species of fish from the Oxford Clay at Christian Malford. *Proceedings of the Geological Society of London*, **4**, 446–449.

KAUFFMAN, E. G. and KESLING, R. 1960. An Upper Cretaceous ammonite bitten by a mosasaur. *Contributions from the Museum of Paleontology, the University of Michigan*, **15**, 193–248.

LEHMANN, U. 1976. *The ammonites: their life and their world*. Cambridge University Press, Cambridge, 245 pp.

MARTILL, D. M. 1985. The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. *Philosophical Transactions of the Royal Society of London, Series B*, **311**, 155–165.

—— 1987. The diet of *Metriorhynchus*, a Mesozoic marine crocodile. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1987**, 621–625.

—— 1988. *Leedsichthys problematicus*, a giant filter-feeding teleost from the Jurassic of England and France, *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **171**, 670–680.

WETZEL, W. 1960. Nachtrag zum Fossilarchiv der Fuiriquina-Schichten. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1960**, 46–53.

WOODWARD, A. S. 1888. On some remains of the extinct selachian *Asteracanthus* from the Oxford Clay of Peterborough, preserved in the collection of Alfred Leeds esq., of Eyebury. *Annals and Magazine of Natural History*, **2**, 336–342.

—— 1892*a*. On the skeleton of a chimaeroid fish (*Ischyodus*) from the Oxford Clay of Christian Malford, Wiltshire. *Annals and Magazine of Natural History*, **9**, 94–96.

—— 1892*b*. On some teeth of new chimaeroid fishes of the Oxford and Kimmeridge Clays of England. *Annals and Magazine of Natural History*, **10**, 13–16.

—— 1893. On the cranial osteology of the Mesozoic ganoid fishes *Lepidotes* and *Dapedius*. *Proceedings of the Zoological Society of London*, **38**, 559–565.

—— 1895. *Catalogue of fossil fishes in the British Museum (Natural History), pt. III, Actinopterygia, Teleostomi*. British Museum (Natural History), London, xxxix + 544 pp., 18 pls.

—— 1896. On the remains of the pycnodont fish *Mesturus*, discovered by Alfred N. Leeds, Esq., in the Oxford Clay of Peterborough. *Annals and Magazine of Natural History*, **17**, 1–15.

—— 1928. A new ganoid fish. *56th Annual Report of the Peterborough Natural History Society*, 59–60, pls. 1–5.

—— 1929. The Upper Jurassic ganoid fish *Heterostrophus*. *Proceedings of the Zoological Society of London*, **99**, 561–566.

DAVID M. MARTILL

Department of Earth Sciences
The Open University
Walton Hall
Milton Keynes, MK7 6AA, UK

Typescript received 12 June 1989
Revised typescript received 31 July 1989